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## Research

### Evolution of searching effort for resources: a missing piece of the puzzle in the ideal free distribution paradigm

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Animals commonly search for information about available resources to select a breeding or foraging site or a mate. Searching can be costly, which is why even random selection of resources may pay off. However, the evolution of searching effort in relation to key ecological factors and its ecological consequences remain insufficiently understood. We build a model to analyze the evolution of searching effort for resources in relation to key ecological factors; the cost of information acquisition, the cost of competition and the distribution of resource qualities. Evolutionarily stable searching effort decreased with increasing cost of information acquisition, eventually resulting in a random choice of resources. With a very low cost of information acquisition, evolutionarily stable searching effort increased with increasing proportion of low-quality resources in the available resource distribution, while the opposite was predicted with a higher cost of information acquisition. Cost of competition had only a negligible effect on the evolution of searching effort, except that increasing cost of competition was biased towards high-quality resources. Informed resource selection (above-zero investment in information acquisition) resulted in skewed distribution of individuals across resources. Consequently, expected fitness became more similar across resources with decreasing cost of information acquisition and associated increase in searching effort, thus approaching the prediction of the classical ideal free distribution (IFD) model stating that individuals distribute themselves so that fitness is invariant across resources. However, we predict a positive correlation between fitness and resource quality with biologically more realistic parameter values, contradicting the IFD model. Costly information acquisition may, thus, explain why IFD is not always found in empirical studies. Generally, our results imply that avoidance of poor choices is more important for the evolution of information acquisition strategies than making the very best choices.

Keywords: competition, evolutionary invasion analysis, habitat selection, mate choice

## Introduction

Animals use resources, such as food, territories, nest sites, shelters and mates in order to gain fitness, and fitness maximization requires acquisition of information on those resources to facilitate selecting the best resources. Information can be gathered directly by personal sampling or indirectly by utilizing the information provided by other individuals. The latter option represents social information use whereby the presence, behavior, decisions and performance of con- and heterospecific individuals (Danchin et al. 2004, Seppänen et al. 2007) provide cues for decision-making. Indeed, information acquisition (personal or social) is a pivotal part of animals' life and it is used in choosing mates (Janetos 1980, Gibson and Höglund 1992, Uy et al. 2001, Byers et al. 2005), foraging patches (Giraldeau and Beauchamp 1999, Luttbeg and Langen 2004), offspring rearing sites (Dale et al. 2006, Mabry and Stamps 2008, Kivelä et al. 2014) and in assessing mortality risk (Emmering and Schmidt 2011, Forsman et al. 2013, Thomson et al. 2013). Irrespective of how information is gathered, the accuracy and the subsequent decisions, likely get better with increasing searching effort. However, investment in searching is costly because of increased mortality and lost opportunities to acquire a territory or mate during searching, with potentially other energetic, physiological and time costs that may negatively affect offspring production and survival (Stamps et al. 2005). Therefore, we expect that searching effort is a behavioral trait under natural selection, and evolves in relation to ecological conditions, provided that there is heritable variation in it.

The first theoretical frameworks about collecting information acknowledged its importance in habitat selection (Fretwell and Lucas 1969, Ward 1987) and mate choice (Parker and Stuart 1976, Janetos 1980) but did not explicitly incorporate searching costs. For example, the bedrock ecological theory, the ideal free distribution (IFD) model by Fretwell and Lucas (1969) assumes, unrealistically, that animals have perfect information about availability of habitat patches and the relationship between patch quality and negative density-dependent effects of competition, and always choose the patch with highest fitness prospects. Because later arriving individuals erode the potential fitness benefits the earlier arrived individuals perceived at the time of settlement decision, all individuals are eventually predicted to have equal fitness. More recent analysis has shown that the IFD can arise also if animals are not omniscient but have local information and tend to disperse to patches with higher fitness payoffs than the recent one (Cressman and Křivan 2006). Hence, information about the quality of available environment is a key mechanism in IFD when the IFD arises as a consequence of choices of individuals (IFD can arise also as a consequence of patch-specific population dynamics (Cressman and Křivan 2006)). Models that include a searching or recognition cost usually have resulted in intuitively correct predictions that increasing costs reduce choosiness of mates, habitat patches or food items (Real 1990, Kotler and Mitchell 1995, Luttbeg 1996, Stamps et al. 2005, Fletcher 2006, Delgado et al.

2013, Cressman et al. 2014, but see Stamps et al. 2005, see also Bocedi et al. 2012 for a reverse choice of emigrating from a habitat patch). Therefore, understanding the benefits and costs of information acquisition is crucial in understanding the decision-making of animals (including human economics; van Raaij 1988) and its implications to mate choice and distribution of individuals in space.

Most models about information acquisition predict that it is a beneficial strategy in most cases (Parker and Stuart 1976, Real 1990, Luttbeg 1996, Boulinier and Danchin 1997, Mönkkönen et al. 1999, Doligez et al. 2003, Stamps et al. 2005, Collins et al. 2006, Fletcher 2006, Lister 2014, Schmidt 2014). Also empirical evidence suggests that information use results in fitness benefits (Forsman et al. 2002, Pärt et al. 2011). However, a few analyses suggest the opposite. Stamps et al. (2005) concluded that the frequency of good and poor habitats and available searching time have much stronger effects on selectivity than mortality cost of searching, while Schmidt's (2014) model emphasized the importance of competition for resources (breeding sites). In another model by Schmidt et al. (2014), investment in searching was predicted to be beneficial only when the information use strategy is rare because increased searching effort result in benefits that increase population size, which in turn increases negative effects of competition that erodes the benefits of increased searching effort. However, information acquisition is clearly an omnipresent and frequent behavior in animals (Doligez et al. 2004, Byers et al. 2005, Dale et al. 2006, Forsman and Thomson 2008, Pärt et al. 2011, Mabry and Stamps 2008). Costs of information acquisition can be substantial (Reid and Stamps 1997, Wickman and Jansson 1997, Okuda 1999, Lin and Batzli 2002, Byers et al. 2005) and plausibly differ among species (Valone and Brown 1989). Therefore, the question which ecological factors affect the observed variation in searching effort among species remains open.

Here, we focus on the evolution of searching effort in relation to intensity and costs of competition, the cost of information acquisition and distribution of resource qualities. Concerning factors that affect the evolution of searching effort, it is obvious that the costs of competition in terms of losing available resources or reproductive opportunities while searching (Kokko 1999, Schmidt et al. 2014) and reduced performance due to resource sharing (Beauchamp et al. 1997) are important. The cost of information acquisition has been acknowledged as well (Real 1990, Luttbeg 1996, Stamps et al. 2005, Fletcher 2006). The distribution of resource qualities also is potentially important for the evolution of searching effort (cf. Boulinier and Danchin 1997, Stamps et al. 2005), especially under the ongoing anthropogenic environmental change that often results in deterioration of the qualities of resources that are necessary for animals. Hence, understanding the potential dependency of the evolution of information acquisition strategies on the distribution of resource qualities, particularly the proportion of high-quality resources out of all available resources, is necessary for predicting biological consequences of environmental change, as well as for assessing the premises of the IFD model.

In our analysis, we assume a resource-based system where the distribution of resource qualities, together with individuals' preferences and performances in relation to resource quality, competition and cost of information acquisition determine the selection regime. We aim to develop a general and heuristic model, with predictions applying to all species and all resource selection contexts, such as mates, food, habitats and safety. Then, we use the framework of evolutionary invasion analysis to examine the evolution of searching effort for resources relative to the key dimensions of the selection regime: distribution of resource qualities, cost of competition and cost of information acquisition. We also investigate the consequences of these dimensions of the selection regime to distribution of individuals across resources and their fitness for comparison to the IFD model.

## The model

We assume a resource-based system, where the resource may be a breeding habitat or territory, a nest site, a mate, a resource for offspring (e.g. a host plant in herbivorous insects) or adult survival (e.g. prey or shelter). We assume that the multidimensional variation of resources that affects fitness can be compressed to a single axis (e.g. a principal component) of resource quality,  $q$ , scaled so that  $0 \leq q \leq 1$ . Therefore, resource quality can, for example, comprise of quality of a habitat patch or territory in terms of match to the niche of the species in question, the quantity and quality of food in the habitat patch or territory, genetic quality and compatibility of a mate, or nutritional quality and size of a host plant or prey.

Individual performance,  $s$ , depends on resource quality. Performance is a major fitness component and can be, for example, offspring survival probability (nest site, breeding territory or host plant selection contexts), adult survival probability (prey or shelter selection contexts), or resource utilization efficiency (foraging decision contexts). Performance is also affected by the number of competitors sharing the same resource, the realized performance due to competition being  $s$  weighted by  $e^{-\omega x}$ , when there are  $x$  competitors present (i.e. the total number of individuals sharing a resource is  $x+1$ ). The parameter  $\omega$  defines the strength of competition. The cost of competition for a given  $x$  increases with increasing value of the parameter  $\omega$  and, given a value of  $\omega$ , the cost of competition increases with increasing number of competitors ( $x$ ) sharing the same resource. We assume that competition is symmetric (i.e. all individuals are equally affected by competition) and can take place only among individuals sharing the same resource. The former assumption aligns with a central assumption of the IFD model (Fretwell and Lucas 1969), and is justified as we analyze the evolution of searching effort, all else being equal. As we consider discrete resources in a system where individuals can use only a single resource at a time, we include no competition between individuals that use different resources.

We assume that the strength of preference for high-quality resources depends on the effort used in assessing the

environment for getting information on resource qualities. We define searching effort,  $E$ , as the proportion of available time or energy used in searching ( $0 \leq E \leq 1$ ). Increasing searching effort results in strengthening preference for high-quality resources, but it is costly because it reduces the time and energy invested in offspring production, parental care or somatic maintenance. Hence, we define the realized performance,  $s(q,x,E)$ , to equal  $q(1 - E^{1/\delta})e^{-\omega x}$ , where  $\delta$  is the cost of information acquisition. The parameter  $\delta$ , thus, determines how fast time and energy available for maintenance and reproduction decrease with increasing searching effort. A  $0 < \delta < 1$  determines a concave function for searching cost (i.e. cost initially accumulates slowly), which seems biologically realistic as information on the qualities of available resources can, to some extent, be acquired along with other behaviors, such as foraging. Searching cost accumulates linearly with increasing searching effort, if  $\delta=1$ , and  $\delta > 1$  defines a convex cost function (i.e. cost initially accumulates rapidly), which we consider biologically unrealistic and, therefore, ignore  $\delta > 1$  in the analysis.

When effort is invested in searching the environment (i.e.  $E > 0$ ), resource acceptance probability must depend on resource quality,  $q$ , so that the probability of accepting a resource increases with increasing resource quality. By following Gomes and Cardoso (2018), we call the function determining resource acceptance probability in relation to resource quality given a searching effort ( $I(q,E)$  in our notation) as the preference function. When no effort is invested in searching for information about resource qualities (i.e.  $E=0$ ), we assume that resources are accepted randomly, that is, resource acceptance probability is 0.5 independently of resource quality,  $q$ , as resources are encountered one at a time in our model. We assume that the preference function  $I(q,E)$  is a linear and increasing function of  $q$ , with a slope equal to  $2E$  when  $E < 0.5$  (Fig. 1). With  $E \geq 0.5$ ,  $I(q,E)$  becomes a sigmoid function that is identical to the preference function by Gomes and Cardoso (2018),  $I(q,E)$  approaching a step function (step at  $q=0.5$ ) with increasing  $E$  (Fig. 1). Thus,  $I(q,E)$  is a combination of a linear function and the function by Gomes and Cardoso (2018), explicitly defined as

$$I(q,E) = \begin{cases} 2Eq + (0.5 - E), & \text{when } E < 0.5 \\ 0.5(2q)^{\frac{E}{1-E}}, & \text{when } E \geq 0.5 \text{ and } q \leq 0.5 \\ 1 - 0.5\left(\frac{1-q}{0.5}\right)^{\frac{E}{1-E}}, & \text{when } E \geq 0.5 \text{ and } q > 0.5 \end{cases} \quad (1)$$

where  $1 - E$  corresponds to  $S$  in the original formulation by Gomes and Cardoso (2018), and we set the  $T$  parameter by Gomes and Cardoso (2018) to 0.5, that is, the inflection point of the sigmoid function is at 0.5. Consequently,  $I(0,E)=0$  and  $I(1,E)=1$  when  $E \geq 0.5$ , which means perfect information for discriminating between the very best and very worst resources, and discrimination between increasing ranges of

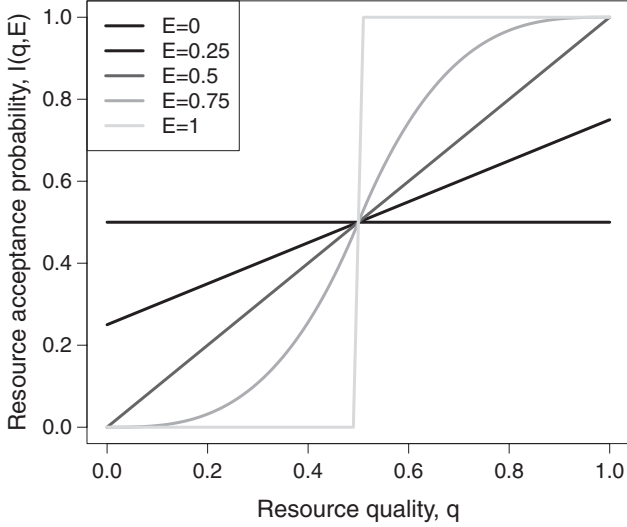


Figure 1. Preference function,  $I(q, E)$ , shown with different values of searching effort  $E$ . The preference function defines the expected probability to accept a resource of quality  $q$ , given a searching effort. As searching effort increases, the preference function becomes steeper and eventually approaches a step function, resulting in an increased probability to accept high-quality resources (i.e. preference for high-quality resources increases) and the probability to accept low-quality resources decreases, that is, discrimination between high-quality and low-quality resources becomes stronger.

high-quality and low-quality resources when  $E$  approaches 1 (Fig. 1). This can be interpreted to align with the assumption of perfect information of the ideal free distribution model (Fretwell and Lucas 1969).

Our model is identical with the ideal free distribution model (Fretwell and Lucas 1969) in the respect that the number of individuals that can share a resource is not constrained but individuals are ‘free’ to choose resources. Despite freedom to choose resources, competition is assumed to take place among individuals sharing the same resource whenever at least two individuals share the same resource.

### Solving evolutionarily stable searching effort

We numerically solved the evolutionarily stable searching effort,  $E^*$ , within the framework of evolutionary invasion analysis (also known as ‘adaptive dynamics’; Diekmann 2004, McGill and Brown 2007). The analysis was done by using the R ver. 4.0.0 (<www.r-project.org>). The R codes of the simulation procedures are available in the Supporting information. As an overview, the analysis proceeded as follows: 1) determining stable population size,  $N^*$ , of a resident population with a particular searching effort,  $E_{res}$ ; 2) introducing a mutant with a particular searching effort,  $E_{mut}$ , into the resident population, 3) simulating population dynamics of the mixed population (residents with the strategy  $E_{res}$  + a mutant with the strategy  $E_{mut}$ ) for one generation and 4) determining consequent fitnesses of resident and mutant strategies in the mixed population. This procedure was repeated 5) so that a full range of mutant strategies (i.e.  $0 \leq E_{mut} \leq 1$ ) was tested

against a full range of resident strategies (i.e.  $0 \leq E_{res} \leq 1$ ). Details are explained below.

To analyze how the qualities of available resources affect the evolutionarily stable searching effort, we repeated the analyses with five different distributions of resource qualities (resource quality distributions, RQDs): uniform, peaked, high-quality biased, low-quality biased and bimodal (Fig. 2). The number of resources,  $R$ , was six in all RQDs to keep computation time within reasonable limits ( $R!$  appears in calculations; see below).

The procedure for finding the evolutionarily stable searching effort was similar for each RQD. First, we calculated the expected fitness of a resident individual in a population consisting of  $N$  resident individuals. We took into account all the  $R!$  ( $= 6! = 720$ ) different orders in which an individual  $i$  ( $i = 1, 2, \dots, N$ ) may meet the available resources. The probability that the individual  $i$  chooses the  $r$ th encountered resource,  $Q_{ir}$ , is

$$Q_{ir} = \begin{cases} I(q_r, E_i), & \text{if } r = 1 \\ I(q_r, E_i) \prod_{t=1}^{r-1} (1 - I(q_t, E_i)), & \text{if } 1 < r \leq R \end{cases} \quad (2)$$

where  $q_r$  is the quality of  $r$ th resource and  $E_i$  is the searching effort of individual  $i$ . The probability for not choosing any of the encountered resources is  $\prod_{t=1}^R (1 - I(q_t, E_i))$ . The probability that individual  $i$  chooses the resource  $k$  ( $k = 1, 2, \dots, R$ ),  $Q_{ik}$ , is the average of the probabilities of choosing this particular resource across the  $R!$  orders of meeting the resources. Second, for each individual, we calculated the probability that the individual  $i$  in question shares the resource  $k$  ( $k = 1, 2, \dots, R$ ) with  $j$  ( $j = 0, 1, \dots, N - 1$ ) other individuals,  $P_{ijk}$ , as

$$P_{ijk} = \begin{cases} Q_{ik} (\prod (1 - Q_{j-k})), & \text{when } j = 0 \\ \sum_{t \in j^+, v \in j^-} Q_{it} (\prod Q_{vt}) (\prod (1 - Q_{vk})), & \text{when } 0 < j < N - 1 \\ \prod_{t=1}^R Q_{it}, & \text{when } j = N - 1 \end{cases} \quad (3)$$

where  $j^+$  is the set of  $N!/(j!(N-j)!)$  individuals that chose the resource  $k$  together with the individual  $i$  and  $j^-$  is the set of  $N - N!/(j!(N-j)! - 1$  individuals that did not choose the resource  $k$  (i.e. all the individuals that remain in the population when individual  $i$  and individuals in the group  $j^+$  are excluded).

Third, we calculated expected fitness for each individual  $i$ ,  $w_i$ , as

$$w_i = \sum_{k=1}^R \sum_{j=0}^{N-1} P_{ijk} q_k e^{-\omega_j} \left( 1 - E_i^{\frac{1}{\delta}} \right) F \quad (4)$$

where  $F$  is number of offspring produced (discounted by  $1 - E_i^{1/\delta}$ ). Note that we must explicitly consider offspring



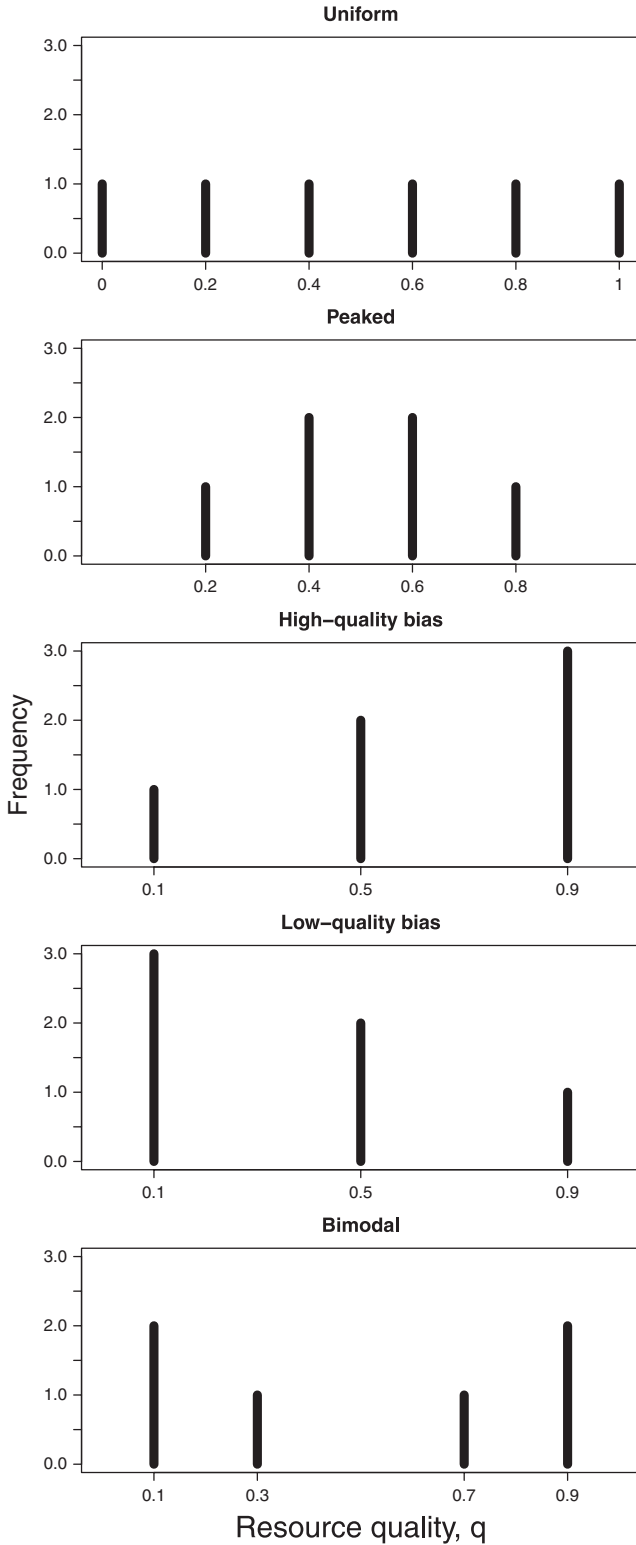


Figure 2. The five distributions of resource qualities (RQDs; from top to bottom: uniform, peaked, high-quality biased, low-quality biased and bimodal distributions) used in the analyses. Resource quality,  $q$ , may vary between 0 (the worst) and 1 (the best), the number of resources being six in each distribution.

production,  $F$  (offspring survival probability is determined by  $q_k e^{-\omega_j}$ ), in this evolutionary invasion analysis where population dynamics need to be modelled. Despite this, the results remain applicable to other resource use contexts. We used  $F=5$  in simulations, but tested if results are sensitive to the value of  $F$  (Supporting information).

Calculating the probabilities  $P_{ijk}$  with the Eq. 3 is computationally very intensive and restricts the manageable population size with standard desktop computers to be very low because the number of different group compositions  $j^*$  for each  $j > 1$  ( $j=0, 1, \dots, N-1$ ) increases explosively with increasing population size. Therefore, we used an approximation for the derivation of the probabilities  $P_{ijk}$  in all analyses. Instead of using the individual-specific probabilities,  $Q_{mk}$ , to describe the probability that an individual  $m$  ( $m \neq i$ ;  $m=1, 2, \dots, N$ ) chooses the resource  $k$  with the individual  $i$  ( $i=1, 2, \dots, N$ ), we used the average of  $Q_{mk}$  calculated across all the  $N$  individuals in the population,  $\bar{Q}_k$ , to describe the probability that any individual  $m$  ( $m \neq i$ ) chooses the resource  $k$  with the individual  $i$ . Consequently, we can approximate  $P_{ijk}$  by  $P'_{ijk}$  calculated as

$$P'_{ijk} = \begin{cases} Q_{ik} (1 - \bar{Q}_k)^{N-1}, & \text{when } j = 0 \\ Q_{ik} \bar{Q}_k^j (1 - \bar{Q}_k)^{N-j-1} \frac{N!}{j!(N-j)!}, & \text{when } 0 < j < N-1 \\ Q_{ik} \bar{Q}_k^{N-1}, & \text{when } j = N-1 \end{cases} \quad (5)$$

and calculate the approximated fitness,  $w_i$ , as

$$w'_i = \sum_{k=1}^R \sum_{j=0}^{N-1} P'_{ijk} q_k e^{-\omega_j} \left( 1 - E_i^{\frac{1}{\delta}} \right) F \quad (6)$$

Relative fitnesses of individuals derived with the accurate (Eq. 3 and 4) and approximation (Eq. 5 and 6) methods are essentially perfectly correlated (Supporting information), so the approximation method does not compromise inferences concerning the evolution of searching effort.

In population dynamics simulations, we assumed a semelparous life history, so population dynamics were modelled with the equation

$$N(t) = \sum_{i=1}^{N(t-1)} w'_i(N(t-1), E_i) \quad (7)$$

where the index  $t$  refers to generation and  $w_i(N(t-1), E_i)$  is the approximated fitness of individual  $i$ , which is a function of population size in the generation where it reproduces and its searching effort (cf. Eq. 5 and 6). Fitness was rounded upwards to the next integer and, if  $\max(w_i) > F$  ( $i=1, 2, \dots, N(t-1)$ ), the vector of approximated fitnesses  $\mathbf{w}$  was rescaled as  $F\mathbf{w}/\max(\mathbf{w})$  (i.e. the maximum fitness set to  $F$ ) and the rescaled fitnesses were then rounded upwards to the next integer.

We started the population dynamics simulations (given values of  $\omega$ ,  $E_{\text{res}}$ ,  $\delta$  and  $F$ ) from five individuals ( $N(0)=5$ ) and continued the simulation until an equilibrium population size was attained (i.e.  $N(t)=N(t-1)$ ), but at most 100 generations. A stable equilibrium was attained within a few generations in most cases. We strived to use parameter values that resulted in equilibrium population sizes below 170 to keep the  $N!$  appearing in the model (Eq. 5) calculable (170! is the limit in R).

We started the evolutionary invasion analysis by solving the equilibrium population size,  $N^*$ , of the resident population along a gradient of the resident strategy,  $E_{\text{res}}$ . The analyzed values of  $E_{\text{res}}$  included those from 0 to 1 with an increment of 0.01, with the values of the cost of information acquisition (parameter  $\delta$ ) ranging from 0.01 to 1 with an increment of 0.01. Next, we added one individual with a searching effort  $E_{\text{mut}}$  into a resident population with  $E_{\text{res}}$ . The analyzed values of  $E_{\text{mut}}$  were the same (from 0 to 1 with an increment of 0.01) as for which the resident equilibrium population sizes were determined. The mixed population including a mutant was of the size  $N^*$  ( $N^* - 1$  residents and a mutant), and the per capita fitnesses of the resident and mutant strategies ( $w_{i_{\text{res}}}$  and  $w_{i_{\text{mut}}}$ , respectively) were then determined in this population. If there were stable cycles in the resident population, a mutant individual was introduced into the resident population at each stage of the cycle and, for both strategies, the per capita fitness was calculated as the geometric mean of the fitnesses attainable in each stage of the population cycle (cf. McGill and Brown 2007).

We tested each of the analyzed mutant strategies against each of the analyzed resident strategies. The mutant strategy was considered as able to invade the resident population, if  $w_{i_{\text{mut}}} > w_{i_{\text{res}}}$ . Otherwise, the resident population was considered to resist the invasion of the mutant. The evolutionarily stable searching effort,  $E^*$ , is that resident strategy ( $E_{\text{res}}$ ) that can resist the invasion of all alternative strategies  $E_{\text{mut}}$  when  $E_{\text{mut}} \neq E_{\text{res}}$ .

### Analyzing variation in evolutionarily stable searching effort

We analyzed how evolutionarily stable searching effort,  $E^*$ , depends on model parameters that describe ecologically important dimensions of the selection regime, that is, 1) the cost of information acquisition ( $\delta$ ), 2) the distribution of resource qualities (RQD; Fig. 2) and 3) the cost of resource sharing (i.e. strength of competition;  $\omega$ ). We solved  $E^*$  along a gradient of  $\delta$  (from 0.01 to 1 with an increment of 0.01; 100 values in total) for each of the five RQDs to assess the influence of ecological variation along dimensions 1) and 2). This procedure was repeated with values of  $\omega$  equaling 0.5 and 1 to assess the effect of competition 3) on the predictions.

Finally, we derived predictions for the distribution of individuals across the resources (i.e. the expected number of individuals sharing a resource of a particular quality) and their expected fitnesses (conditional on selecting a resource of a particular quality) in a (resident) population adopting the strategy  $E^*$ . This was done as explained above, except that we

focused on population-level probabilities (instead of individual-level probabilities as explained above) of finding a certain number of individuals on a certain resource. Consequently, the approximated probability that  $j$  ( $j=1, 2, \dots, N^*$ ) individuals share resource  $k$ ,  $B'_{jk}$ , was calculated as

$$B'_{jk} = Q_k^j (1 - Q_k)^{N^* - j} \frac{N^*!}{j!(N^* - j)!} \quad (8)$$

where  $Q_k$  is the probability that an individual following the strategy  $E^*$  in a resident population chooses the resource  $k$  ( $k=1, 2, \dots, R$ ). Equation 8 was used instead of Eq. 5 in the derivation of probability weights for calculating the expected number of individuals sharing the resource  $k$  and expected fitness on that resource (i.e.  $P'_{ijk}$  in Eq. 6 was replaced by  $B'_{jk}$ ).

## Results

Evolutionarily stable searching effort,  $E^*$ , gradually decreased from a non-zero value to zero with increasing cost of information acquisition,  $\delta$ , with each distribution of resource qualities (RQD; Fig. 3, Supporting information). When the parameter  $\delta$  was above ca 0.75 (the exact value depends on RQD),  $E^*$  was invariably zero (Fig. 3). Consequently, resource selection strategy changed from informed to random with increasing cost of information acquisition. With very low cost of information acquisition ( $\delta < 0.2$ ),  $E^*$  was highest when RQD was low-quality biased, followed by bimodal and uniform RQDs, the proportion of low-quality resources in the RQD decreasing across these RQDs in this order. In high-quality biased RQD,  $E^*$  remained relatively low ( $< 0.4$ ) even with a very low cost of information acquisition, which is understandable because the probability of choosing a high-quality resource from such an RQD remains relatively high even if choices were random. Hence,  $E^*$  seems to increase with increasing proportion of low-quality resources in the RQD (i.e. risk of choosing a low-quality resource if choices were random) when the cost of information acquisition is very low. With peaked RQD, there was no evolutionarily convergent stable  $E$  with very low cost of information acquisition ( $\delta < 0.17$ ; Supporting information; only convergent stable  $E^*$  are shown in Fig. 3) but otherwise, with this RQD, the predicted  $E^*$  was among the lowest ones across the analyzed gradient of cost of information acquisition.

Interestingly, the rank order of RQDs in terms of  $E^*$  changed with increasing  $\delta$ . When  $\delta > 0.4$ , the highest  $E^*$  was predicted in uniform and high-quality biased RQDs and lowest in low-quality-biased and peaked RQDs (Fig. 3). This implies that avoidance of poor choices is important for the evolution of searching effort, because even a relatively low searching effort considerably reduces the probability to choose low-quality resources when low-quality resources are rare in the RQD, while a high searching effort would be required for the same effect when low-quality resources are abundant in the RQD, the associated cost outweighing the benefits when

$\delta$  is high. On the other hand, the uniform RQD was the only RQD that included the extremes of resource quality, 0 and 1, and the highest  $E^*$  predicted with this RQD was 0.5.  $E^* \geq 0.5$  results in probabilities of 0 and 1 to choose resources of quality 0 and 1, respectively. This prediction, thus, suggests that either discrimination of the poorest choices or ensuring the very best choices drives the evolution of searching effort. To get more insight into this, we repeated the analysis with the uniform RQD so that we, in turn, left out the resource of quality 0 and 1. With decreasing  $\delta$ ,  $E^*$  rose to 0.5 when the resource of quality 1 was left out of the analysis and to 0.3 when the resource of quality 0 was left out (Supporting information), indicating that discrimination of the poorest resources strongly affects the evolution of searching effort.

The strength of competition among individuals sharing a resource,  $\omega$ , mainly had a negligible effect on  $E^*$ , with the exception of high-quality biased RQD where strengthening competition clearly increased  $E^*$  when  $\delta < 0.4$  (Fig. 3). However, increasing cost of competition strongly reduced population size, resulting in decrease of the expected number of individuals per resource with increasing  $\omega$  (Supporting information).

The distribution of individuals across resources increasingly biased towards high-quality resources with decreasing cost of information acquisition (i.e. with decreasing  $\delta$  and consequently increasing searching effort,  $E^*$ ) in all RQDs, while random choice of resources (i.e.  $E^*=0$ , associated with  $\delta$  close to one) resulted in even distribution of individuals across resources (Supporting information), as expected. This had fitness consequences, expected fitness being relatively equal across resource quality classes with low cost of information acquisition, but increasing cost of information acquisition introduced a positive relationship between resource quality and expected fitness, this relationship becoming steeper with increasing cost of information acquisition (Fig. 4, Supporting information). The relatively low variation in expected fitness across resources with a very low cost of information acquisition (i.e. when ‘perfect’ information sensu Fretwell and Lucas (1969) is attainable) can be seen to approach the key prediction of equal fitness across resources of the IFD model (Fretwell and Lucas 1969).

## Discussion

Our model predicts that investment in information acquisition evolves in relation to cost of information and the distribution of resource qualities (i.e. resource quality distribution, RQD), while the strength of competition for the shared resource seems unimportant in most cases. Decreasing investment in searching effort for resources with increasing cost of information acquisition is a logical result and in accordance with earlier analyses (Real 1990, Kotler and Mitchell 1995, Luttbeg 1996, Fletcher 2006, Bocedi et al. 2012, Delgado et al. 2013, Cressman et al. 2014, but see Stamps et al. 2005, Schmidt 2014). On the other hand, informed resource selection led to skewed distribution of

individuals across resources, most individuals choosing high-quality resources, which smoothed fitness variation across resources. When the cost of information acquisition approached zero, variation in expected fitness across resources decreased, which approaches the prediction of equality of fitness across resources under the classical ideal free distribution (IFD) model (Fretwell and Lucas 1969). However, relaxing the key assumption of the IFD model – perfect information on resource qualities – and instead more realistically assuming that the acquisition of information is costly changes the predictions by introducing a positive correlation between resource quality and fitness. A positive correlation between resource quality and fitness better matches the prediction of the ideal despotic distribution (IDD) for resource monopolization by Fretwell and Lucas (1969) than the IFD model, even if individuals are free to choose among resources (see Table 1 for a comparison of predictions of the IFD, IDD and present models).

Our analysis suggests that a relatively high proportion of low-quality resources in RQD is most favorable for the evolution of high searching effort for resources. This prediction aligns with that of Boulinier and Danchin (1997) but contradicts those of Stamps et al. (2005) who predicted that selectivity increases with increasing frequency of high-quality habitats and with increasing quality difference between high- and low-quality habitats. The predictions of our model complement this apparent contradiction by showing the

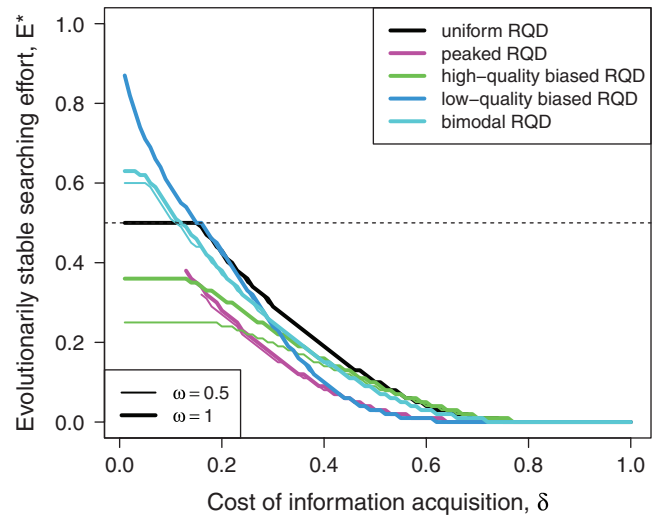


Figure 3. Evolutionarily stable searching effort,  $E^*$ , in relation to the cost of information acquisition,  $\delta$ , with uniform (black), peaked (magenta), high-quality biased (green), low-quality biased (blue) and bimodal (turquoise) distributions of resource qualities (RQDs). Within each distribution of resource qualities, the line width illustrates the cost of resource sharing, thin and thick lines indicating low ( $\omega=0.5$ ) and high ( $\omega=1$ ) cost of resource sharing, respectively. With peaked distribution of resource qualities, there was no convergent stable ESS with low values of  $\delta$ , which is why the red lines do not extend to the lowest values of  $\delta$ . The horizontal dashed line indicates the transition from a linear ( $E \leq 0.5$ ) to a sigmoid ( $E > 0.5$ ) shape of the preference function.



interaction between RQD and cost of information acquisition as the predictions reverse along the cost-of-information-acquisition dimension in our analysis. When the cost of information acquisition is low ( $\delta < 0.2$ , Fig. 3), the highest searching effort was predicted to evolve under RQDs where high-quality resources are rare (in particular, in low-quality biased RQD). Then, it pays to invest in information acquisition because it increases the probability of choosing a high-quality resource. An increasing investment in information acquisition, however, translates into increasing aggregations of individuals on the best resources, which increases the realized costs of resource sharing (i.e. costs of competition), consistent with Schmidt et al. (2014). If the RQD is such where the probability of choosing a high-quality resource is high by chance (e.g. high-quality biased RQD), the costs of resource sharing due to individuals aggregating on best resources outweigh earlier the benefits of high baseline performance on those resources, explaining why a relatively low searching effort is favored when high-quality resources are abundant and  $\delta < 0.2$ . On the other hand, when cost of information acquisition is higher ( $0.4 < \delta < 0.6$ ; Fig. 3), a relatively high searching effort pays off when high-quality resources are abundant to avoid selecting low-quality resources despite increasing associated costs of resource sharing on best resources (Supporting information), consistent with Stamps et al. (2005). However, when high-quality resources are rare (e.g. low-quality biased RQD) and  $0.4 < \delta < 0.6$ , costs of resource sharing rapidly outweigh the benefits of increasing searching effort because a relatively high searching effort (and cost) would be required for the avoidance of selecting low-quality resources. Hence, RQD and costs of information acquisition and resource sharing appear important for the evolution of searching effort.

Generally, the relative importance of competition in the evolution of resource selection strategies seems controversial. While our model predicts a negligible competition effect on the evolutionarily stable effort invested in information acquisition in all except high-quality biased RQD (Fig. 3), others have predicted competition to be important for the evolution of resource selection strategies (Real 1990, Mönkkönen et al. 1999, Schmidt 2014, Schmidt et al. 2014). Despite a generally negligible competition effect on the evolutionarily stable searching effort in our analysis, increasing cost of competition substantially reduced the expected numbers of individuals sharing a resource due to reduced population size and resulted in more uniform distribution of individuals across resources (Supporting information; Beauchamp et al. 1997). When the expected number of individuals sharing a resource decreases, the realized cost of competition due to resource sharing also decreases. Because of this ecological (population dynamics) feedback loop, selection regime affecting the evolution of searching effort remains only little affected by competition (but see Schmidt et al. 2014).

In our analysis, share of resources was free, which aligns with the central assumption of the IFD model (Fretwell and Lucas 1969), and resulted in a positive correlation between the expected number of individuals sharing a resource and resource quality when resource selection was informed

(Supporting information), consistently with the IFD model. However, expected fitness showed some variation across resources even when practically perfect information on resources was attainable (i.e. cost of information acquisition was negligible), contradicting the central prediction of the IFD model. In our modeling framework, the definition for perfect information is, nevertheless, not equal to that used by Fretwell and Lucas (1969), who assumed that individuals are perfectly aware of the fitness consequences of choices, which may explain the discrepancy between the predictions. Yet, imperfect information may also result in IFD in habitat patch selection context if individuals preferentially migrate to more profitable patches (Cressman and Křivan 2006). Hence, we may conclude that our predictions approach those of the IFD model when cost of information acquisition approaches zero. With biologically more realistic cost of information acquisition, expected fitness was positively correlated with resource quality (Fig. 4), matching with the prediction of the IDD model for resource monopolization. We suggest that cost of information acquisition may explain why IFD is not always found in empirical studies.

We developed a general and heuristic model that includes a probabilistic choice among multiple resources. Our model is applicable in all resource selection contexts, which contrasts to many earlier approaches that have been tailored for specific systems, processes or species, such as habitat or territory selection (Boulinier and Danchin 1997, Mönkkönen et al. 1999, Doligez et al. 2003, Stamps et al. 2005, Fletcher 2006, Delgado et al. 2013, Schmidt 2014, Schmidt et al. 2014), foraging patch selection (Bernstein et al. 1991, Beauchamp et al. 1997), food item selection (Kotler and Mitchell 1995, Cressman et al. 2014) or mate choice (Janetos 1980, Real 1990, Luttbeg 1996, Collins et al. 2006). Our probabilistic resource selection also brings about more biological realism compared to the deterministic choice in the IFD model (Fretwell and Lucas 1969) because there is typically wide quality variation in real resources and uncertainty is likely always present in the assessment of true resource quality. Furthermore, some earlier analyses include only two types of resources (Kotler and Mitchell 1995, Mönkkönen et al. 1999, Doligez et al. 2003, Stamps et al. 2005, Cressman et al. 2014, Schmidt et al. 2014), which limits generality. The threshold rule of resource selection, which is used in many analyses (Janetos 1980, Real 1990, Luttbeg 1996, Collins et al. 2006, Schmidt 2014), may be too simplistic for many real systems. Our analysis with probabilistic resource selection appears a more realistic generalization of the threshold rule and includes the strict threshold rule as a limit when searching effort approaches one (Fig. 1).

## Conclusions and implications

Our results highlight the importance of RQD for the evolution of searching effort (Boulinier and Danchin 1997, Stamps et al. 2005). When information is cheap, natural selection favors a high effort in information acquisition if high-quality resources are rare, while more costly information

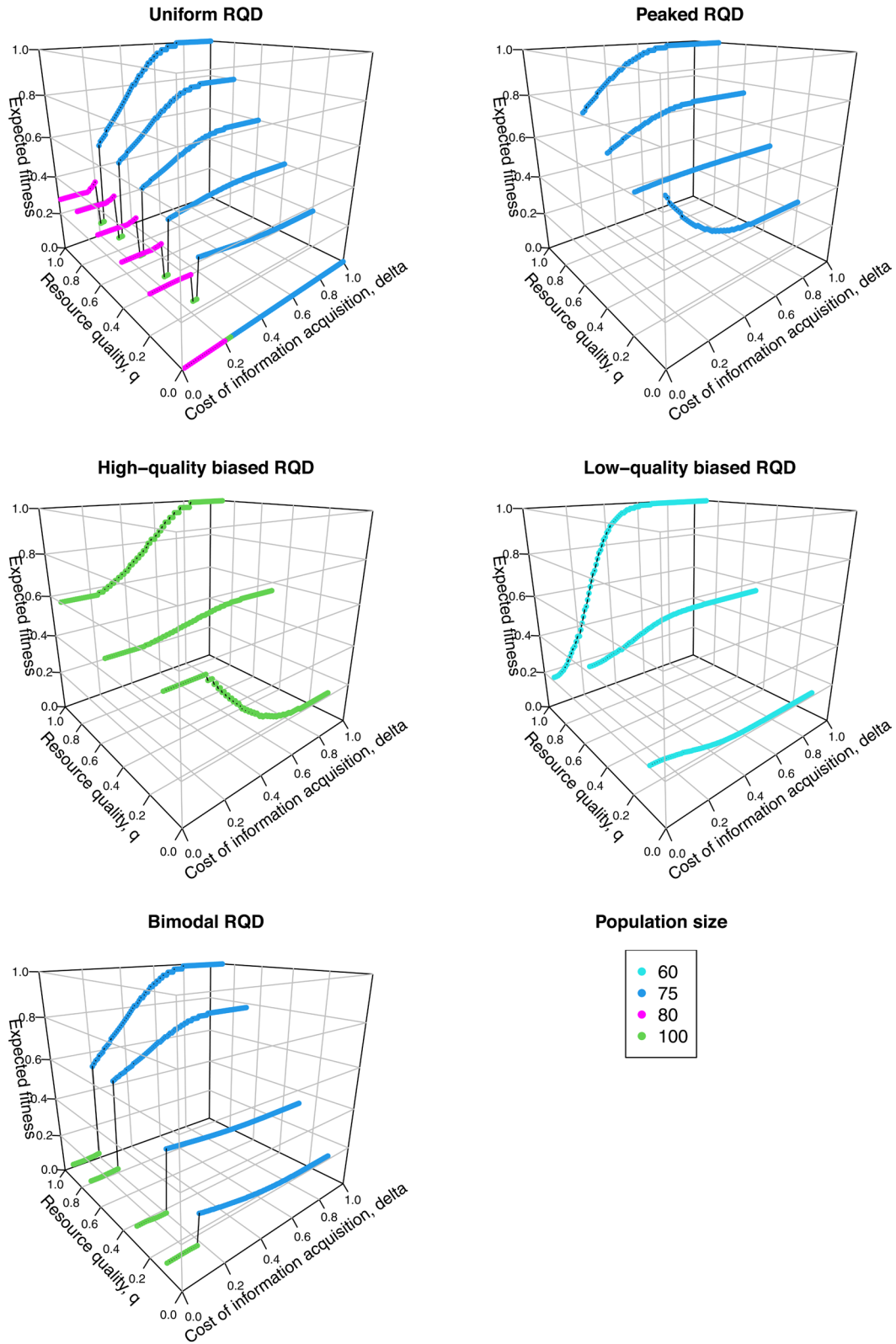


Figure 4. Expected fitness (scaled so that maximum fitness is 1) in different resource quality classes (colored points connected with a thin black line) in relation to the cost of information acquisition,  $\delta$ , in populations where the evolutionarily stable searching effort ( $E^*$ ) prevails. Each distribution of resource qualities (RQD) is presented in different panel. The color of the points indicates the equilibrium size of the monomorphic population where the evolutionarily stable searching effort prevails. Note that the discontinuities in uniform and bimodal RQDs appear because changing equilibrium population size (equilibrium population size depends on both  $\delta$  and  $E$ ; Supporting information) affects the expected number of individuals sharing the resources (Supporting information), which, in turn, affects the realized cost of resource sharing and so expected fitness. Other parameter values were:  $\omega = 0.5$ ,  $F = 5$ .

Table 1. Comparison of the predictions of the ideal free distribution (IFD) and ideal despotic distribution (IDD) models by Fretwell and Lucas (1969), and the present model. Because the predictions of the present model depend on the cost of information acquisition, we present those predictions both for negligible ( $\delta < 0.2$ ) and non-negligible ( $\delta > 0.3$ ) cost of information acquisition.

	IFD	IDD	Present model	
			Negligible cost of information acquisition	Non-negligible cost of information acquisition
Fitness	equal among resources	positively correlated with resource quality	approximately equal among resources <sup>a</sup>	positively correlated with resource quality
Number of individuals	positively correlated with resource quality	positively correlated with resource quality, yet number of individuals varies less across resources than in IFD	positively correlated with resource quality	positively correlated with resource quality, but becomes equal across resources with increasing cost of information acquisition

<sup>a</sup> Depends on distribution of resource qualities (RQD); fitness varies somewhat more across resources on some RQDs (Fig. 4, Supporting information), but always much less than with higher cost of information acquisition.

reverses the prediction and a relatively high effort in information acquisition is expected when high-quality resources are abundant. This is a testable prediction and implies that avoidance of poor choices is more important for the evolution of information acquisition strategies than making the very best choices (Supporting information), which can be seen as a form of evolutionary bet hedging (cf. Seger and Brockmann 1987, Starrfelt and Kokko 2012). To which degree poor choices can be avoided depends on RQD and the cost of information acquisition; avoidance of poor choices can be attained with relatively low searching effort when high-quality resources are abundant, while it requires a high searching effort in the opposite case.

In other contexts, the economic prospect theory (Kahneman and Tversky 1979) and cumulative prospect theory (Tversky and Kahneman 1992) predict risk aversion in humans; we rather avoid losses than aim for gains (that include an inherent risk) of the same value. Similar behavior occurs also in capuchin monkeys *Cebus apella* (Silberberg et al. 2008, Lakshminarayanan et al. 2011). In passerine birds, in interspecific social information use context, avoiding and rejecting the apparent choices of low quality tutoring birds that plausibly make poor decisions is stronger than copying the choices of high quality tutors that apparently have made good decisions (Forsman and Seppänen 2011, Seppänen et al. 2011, Loukola et al. 2013). Hence, emphasis in avoiding poor decisions and losses rather than aiming at good decisions and gains may be a universal behavioral strategy in the animal kingdom.

Our probabilistic model provides new insight in distribution of animals in space and its ecological implications. Contrary to the IFD model, but consistent with the IDD model, a positive correlation between fitness and resource quality is typically expected even when individuals are free to share resources and aggregate on the best resources (Table 1). This is the second empirically testable prediction of our model; individuals making informed choices should aggregate on the best resources so that the number of individuals is positively correlated with resource quality and the fitnesses of these individuals are also positively correlated with resource quality if information is costly. This prediction has implications for social information use (Seppänen et al.

2007, Gil et al. 2018). If density of aggregated individuals honestly reflects resource quality, copying the choices of the majority pays off. Accordingly, some birds are known to be attracted to high density of either conspecifics (Serrano and Tella 2003) or heterospecifics (Forsman et al. 2008) when selecting a breeding site.

Finally, our results imply that animal information use strategies are expected to respond to anthropogenic environmental changes, that often result in habitat deterioration (Amo et al. 2007, Pike et al. 2010), and so increase the frequency of low-quality resources in the RQD. All else being equal, and assuming costly information acquisition, habitat deterioration should select for decreased searching effort according to our model. Anthropogenic habitat deterioration or other environmental changes may result in an ecological or evolutionary trap if they decouple cues that used to indicate resource quality from the present fitness payoff or by producing novel cues, resulting in maladaptive resource choices (Fletcher et al. 2012, Robertson et al. 2013, Hale and Swearer 2016). For example, even though habitat degradation may not change the proximate cues used by animals, it may negatively affect the fitness value of the resource, for example by lowering the survival (Robertson and Hutto 2007, Hawlena et al. 2010). Human activities may also distort old cues. Remeš (2003) showed that changed plant phenology in areas dominated by non-native plant species gave a false impression of high-quality breeding habitat for breeding birds, breeding success being low in those areas. It seems realistic to expect that a high investment in information acquisition is required to discriminate between resources forming evolutionary traps and high-quality resources (e.g. learning to use novel indicators of resource quality). Reflecting the predictions of our model on this, we would expect selection for increasing searching effort in the beginning of environmental change (e.g. habitat deterioration) when resources forming traps are rare, and less selection for it when trap resources become abundant (i.e. RQD becomes dominated by low-quality resources). Given the pace of anthropogenic environmental change, there may not be enough time for an evolutionary response in the beginning of the process. Unless phenotypic plasticity does not facilitate a switch to different sources of

information, our analysis paradoxically predicts that selection favors low or zero investment in information acquisition if poor resources become dominant and information is costly to acquire, which enhances trapping (Robertson et al. 2013). This remains to be empirically tested.

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### Author contributions

**Jukka T. Forsman:** Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Resources (equal); Software (supporting); Supervision (equal); Validation (supporting); Visualization (supporting); Writing – original draft (equal); Writing – review and editing (equal). **Sami M. Kivela:** Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (equal); Methodology (lead); Project administration (equal); Resources (equal); Software (lead); Supervision (equal); Validation (lead); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal).

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